The importance of the cloacal bursae as the primary site of aquatic respiration in the freshwater turtle, *Elseya albagula*

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ABSTRACT

The ability of freshwater turtles to exchange respiratory gases with their aquatic environment is well known and facilitates prolonged dive durations among several species. Three main sites have been implicated in aquatic respiration (skin, cloaca and buccopharynx) yet the relative contribution of each to total aquatic O_2 uptake has been poorly examined among Australian chelids. In this study we investigated the diving physiology of *Elseya albagula*, a bimodally respiring turtle from Queensland, Australia. Through partitioning experiments we tested the hypothesis that the cloacal bursae are the main site of aquatic O_2 uptake in this species. Aquatic oxygen uptake accounted for 70 ± 8% of total oxygen requirements demonstrating the impressive ability of the species to respire underwater, although this was negatively correlated with body mass. Further, the cloacal bursae were found to account for 48% of total aquatic oxygen uptake, providing strong evidence that they are the primary site of aquatic respiration in *E. albagula*.

Key words: Diving; Reptile; Bimodal Respiration; Physiology; Mary River; Oxygen Consumption; Metabolic Rate; Bimodal Breathing

Introduction

The contemporary reptilian fauna of Australia comprises approximately twenty species of freshwater turtles, several of which have a highly aquatic lifestyle and are known only to leave the water to lay eggs (Legler and Georges 1987). Because the duration of dives in freshwater turtles is thought to be primarily limited by oxygen availability and consumption rate (Santos *et al.* 1990), one of the most important physiological challenges they face is that of oxygen uptake and efficiency in its utilisation. A number of physiological adaptations have been identified which enable freshwater turtles to extend periods of submergence, including cardiorespiratory adjustments resulting in decreased O_2 consumption (Andersen 1966; Belkin 1968; Smith and Charvalho 1985; Ware 1993; Wang and Hicks 1996), the depression of metabolic rate (Jackson 1968; Caligiuri *et al.* 1981), and the utilisation of anaerobic metabolism (Jackson 1968; Gatten 1981; Schmidt-Nielson 1983).

To extend dive duration, many freshwater turtles also possess the ability to exchange respiratory gases in both air and water and are therefore known as bimodal breathers (Belkin 1968; Jackson *et al.* 1976; Gatten 1980, 1984; Stone *et al.* 1992a, b; Priest 1997). The exchange of gases with the aqueous environment is commonly referred to as aquatic respiration. The ability to respire aquatically allows bimodal breathing turtles to undertake extended dives and may confer several ecological benefits. It has been suggested that the use of aquatic respiration may reduce overall energetic expenditure, reduce exposure to threats during surfacing events, and facilitate the exploitation of fast-flowing habitats such as riffle zones (Tucker *et al.* 2001; Maina 2002; Gordos 2004; Mathie and Franklin 2006; Storey *et al.* 2008).

Aquatic respiration in freshwater turtles has been examined in numerous studies, many of which have attempted to quantify this respiratory ability in a variety of turtle species and to determine the major sites involved in aquatic respiration (e.g. Root 1949; Dunson 1960; Jackson 1976; Gatten 1980, 1984; King and Heatwole 1994a, b; Bagatto *et al.* 1997). Three main areas have been implicated in non-pulmonary gas exchange: the skin, buccopharyngeal cavity, and cloacal bursae. The cloacal bursae are paired dorso-lateral sac-like evaginations of the cloaca. Within Australian freshwater turtles there is considerable interspecific variation in the degree to which the cloacal bursae are specialised for respiratory gas exchange, especially with regards to the relative size of the bursae and the extent to which they are lined with papillae that increase effective surface area (Legler 1987; Legler and Georges 1987). Through rhythmical contraction of the cloacal muscles the bursae and papillae are ventilated with freshwater, facilitating exchange of respiratory gases with the aqueous environment (Priest 1997; Franklin 2000; Priest and Franklin 2002; Gordos and Franklin 2002; Clark *et al.* 2008a, b; Clark *et al.* 2009).

The cloacal bursae are known to be important sites of aquatic respiration in several species of Australian freshwater turtles, including the Fitzroy River Turtle *Rheodytes leukops*, the Mary River Turtle *Elusor macrurus* and a recently described snapping turtle *Elseya albagula* (Legler and Cann 1980; Legler 1987; Priest 1997; Franklin 2000; Limpus *et al.* 2002; Clark *et al.* 2008a, b). The cloacal bursae of *R. leukops* are considered the most specialised among Australian chelids as they are lined with papillae that are highly vascularised and multi-branching (Legler and Cann 1980; Legler 1987; Priest 1997). Consequently, the ability

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to respire aquatically is thought to be most advanced in *R. leukops*, which has been shown to have an average reliance on this mode of O_2 exchange ranging from approximately 40% in adults to 73% in juveniles (Priest 1997; Clark *et al.* 2008a). Further, dive durations of *R. leukops* are the longest recorded for any Australian chelid, ranging from an average 38min in adults to 839min in juveniles and occasionally exceeding two days duration (Priest and Franklin 2002; Gordos *et al.* 2006; Clark *et al.* 2008a).

The cloacal bursae of the snapping turtle *Elseya albagula* are also highly specialised and completely covered in branched but flattened papillae (Figure 1; Legler and Cann 1980; Legler 1987; Limpus *et al.* 2002), suggesting they are less specialised for aquatic gas exchange than the bursae of *R. leukops*. Laboratory investigations of the diving physiology of *E. albagula* support this assertion, with adult and juvenile turtles shown to have a lower reliance upon aquatic respiration than *R. leukops* (mean 17% and 14% respectively; Mathie and Franklin 2006; Clark *et al.* 2008a). Further, while mean dive duration in adult *E. albagula* (35min) is reportedly similar to that for *R. leukops* (38min), juvenile *E. albagula* have a greatly reduced mean dive duration (24min v 839min *R. leukops*: Mathie and Franklin 2006; Clark *et al.* 2008a). Despite this, several studies have reported captive and wild *E. albagula* undertaking dives in excess of three hours duration highlighting the impressive diving ability of this species, which is likely attributable to its aquatic respiration capabilities (FitzGibbon 1998; Gordos *et al.* 2007; Clark *et al.* 2008a; Storey *et al.* 2008).

Although many studies have examined the importance of aquatic respiration in Australian freshwater turtles, only two studies have attempted to quantify the relative contribution of extrapulmonary sites of gas exchange to overall aquatic respiration. King and Heatwole (1994a) found that in the Australian saw-shelled turtle *Elseya latisternum*, mean aquatic O_2 uptake represented an average 27% of total oxygen consumption at 20°C. From partitioning experiments, whereby areas of extrapulmonary gas exchange were selectively blocked, King and Heatwole (1994a) concluded that the buccopharyngeal cavity was of primary importance in *E. latisternum* with almost half (49%) of all aquatic respiration occurring via this route. They found cloacal respiration accounted for 33% of total aquatic O_2 uptake, and the remaining 18% was attributed to gas exchange across the skin. In the only other examination of the relative importance of extrapulmonary sites of respiration in Australian freshwater turtles, Priest (1997) determined that the cloaca was the main site of aquatic gas exchange in *R. leukops*, accounting for an average 68% of total aquatic O_2 uptake. This high reliance upon cloacal gas exchange in *R. leukops* likely reflects the highly specialised morphology of the cloacal bursae in the species. The relative importance of non-pulmonary respiratory surfaces has not been quantified in any other Australian chelids, although it is widely presumed that the cloacal bursae are of primary importance for aquatic oxygen exchange in most bimodally breathing species.

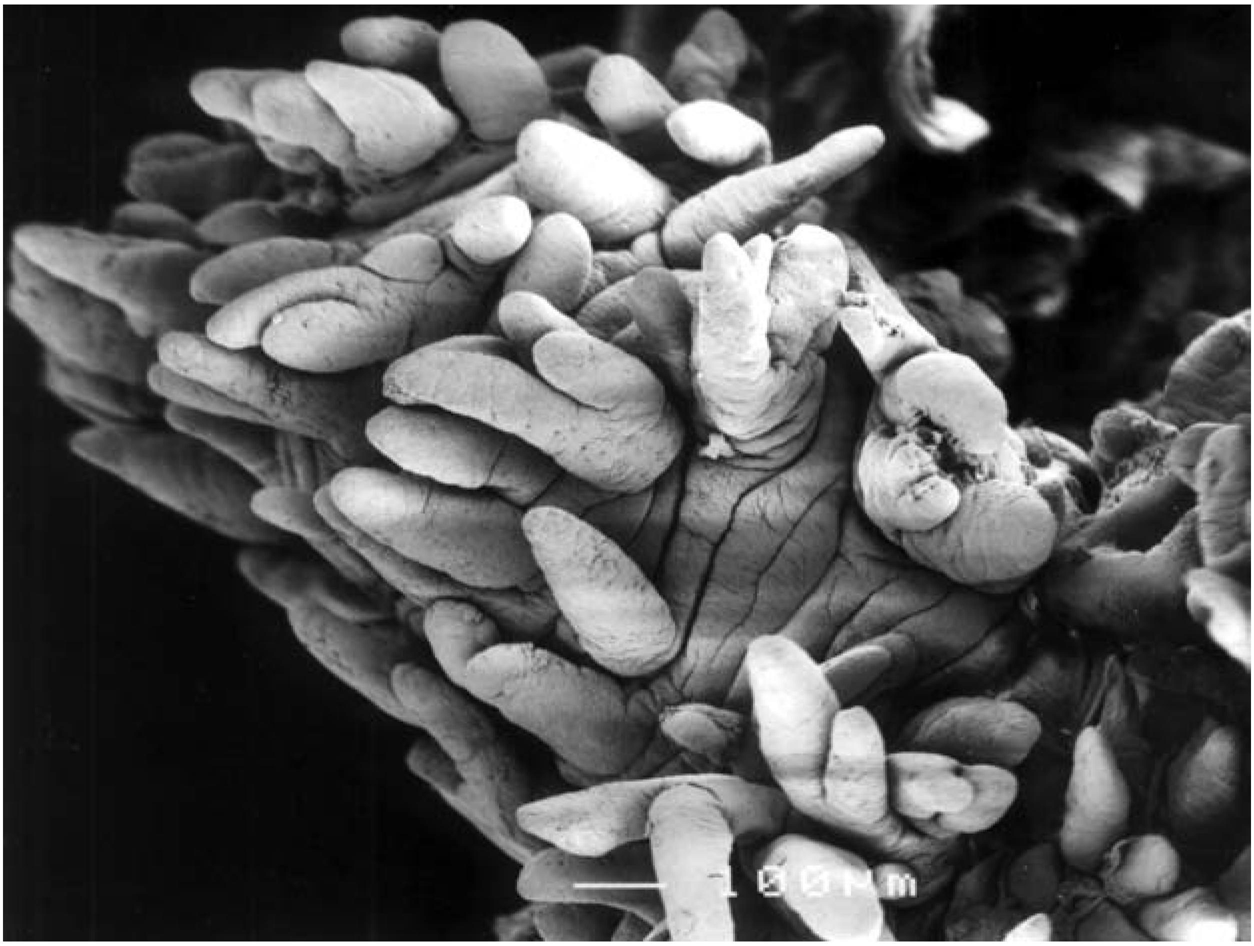

Figure 1. Micrograph of the branched papillae lining the cloacal bursae of *Elseya albagula*.

In this study we tested the hypothesis that the cloacal bursae are the main site of aquatic respiration in *E. albagula*, a freshwater turtle from Queensland that is known to be a bimodal breather. Specifically, our objectives were to 1. Quantify the contribution of aerial (pulmonary) and aquatic (extrapulmonary) gas exchange to overall respiration, and 2. Quantify the contribution of cloacal gas exchange to overall aquatic respiration.

Methods

Collection and maintenance of study animals

Elseya albagula is a freshwater turtle known from the Mary, Burnett and Fitzroy River drainages on the east coast of Queensland (Thomson *et al.* 2006). It is a large short-necked Chelid, with adult females attaining lengths of up to 40 cm (SCL) and body masses in excess of 6.5 kg while mature males are substantially smaller. In their natural habitat, individuals are usually encountered at rest, concealed in submerged log jams or rock crevices on river bottoms (Gordos *et al.* 2007; FitzGibbon pers. obs.). Animals show a preference for deeper (2-6 m depth) sections of the rivers often with a steeply inclined underwater bank (Limpus *et al.* 2002; Gordos *et al.* 2007).

Study animals were collected from a 2 km stretch of the Mary River (nr. Gunalda) by snorkelling through the deeper pools and searching around submerged logs and rock crevices. The turtles were transported to The University of Queensland animal holding facility where they were housed in large plastic tanks (200 l). A full spectrum Reptiglow light was suspended above each holding tank and maintained on a photoperiod of 12L:12D. Water depth varied between 30-60 cm and was continuously filtered and aerated, and changed regularly. Wooden platforms were suspended just above the water surface but animals were rarely seen basking (3 occasions during 9 months). Turtles preferred to hide beneath the platforms or under large logs placed in the tanks. The turtles were fed two to three times weekly, depending upon the voraciousness of their appetite and the time of year. After trialling several fruits, vegetables, plants and meats it was found the animals preferred a diet of chopped paw-paw and aquatic macrophytes (e.g. *Vallisneria* sp.) collected from their natural habitat, supplemented with diced sheep livers and boiled carrots.

Partitioning of total oxygen consumption

Aerial and aquatic oxygen consumption was simultaneously measured in five freely diving *E. albagula* (mean mass 2.43 kg, range 0.68 - 4.3 kg). Experiments were conducted in a controlled temperature room where water temperature was maintained at 22ºC and the photoperiod was 12L:12D. All experiments were performed during daylight hours. The turtles were allowed at least two days to acclimate to the chosen temperature, and were fasted for 5-7 days prior to experiments.

Immediately before each experiment was commenced, the turtle subject was wiped thoroughly with a towel to dry the skin and shell, after which it was swabbed with 70% alcohol to reduce the possible consumption of oxygen by bacteria. The turtle was then left to dry in a container for 20-30 min before being washed down with distilled water. The turtle was then placed in the respirometry chamber, consisting of a water-filled, black Nally bin (50 l) with a clear Perspex lid containing a smaller air-filled compartment (aerial chamber) into which the animal could surface.

The aerial chamber acted as a flow-through respirometry system and was fitted with an inlet and outlet port. The inlet port was connected to a cylinder of compressed air and the outlet port was connected to a Servomex paramagnetic O_2 transducer and analyser (series 1100), which recorded the fractional concentration of O_2 in the outgoing air. Before entering the paramagnetic O_2 analyser the outgoing air passed through H_2O absorbing Drierite and CO_2 absorbing soda lime and then an Omega electronic flowmeter (model FMA-5610) which ensured air flow through the surfacing chamber was maintained at 150 ml min^{-1}.

The Nally bin itself acted as a closed-box respirometry chamber, and was filled with O_2 saturated water at 22ºC just prior to each experiment. Once the experimental turtle had been placed in this base chamber the clear Perspex lid was bolted to the upper lip of the Nally bin and a lining of dried, non-toxic silicone acted as a gasket ensuring an air tight seal. To remove trapped O_2 from the base chamber a set of aquarium cleaning magnets was used to drag air bubbles to the surfacing chamber. The air-water interface was covered with a thin layer of mineral oil to retard the movement of gases between the aquatic and aerial phases. Mineral oil does not appear to interfere with the respiratory surfaces of freshwater turtles (King and Heatwole 1994a). A black cloth was then placed over the entire Perspex lid but with a hole cut to accommodate the aerial compartment and expose it to light. The cloth served to calm the animal and assist it in locating the illuminated surfacing chamber. A bucket fitted with an internal 12V light bulb was then placed over the aerial chamber to minimise disturbance to surfaced animals from experimenter movement within the controlled temperature room. Thirty minutes after the turtle was placed in the respirometry chamber the first water sample was withdrawn from a sampling port fitted with a three-way valve. The sample was then injected into a Cameron O_2 microelectrode and PO_2 was measured using a Cameron oxygen meter (model OM200), calibrated using water saturated with oxygen (upper end) and then nitrogen (lower end). Water samples were collected from the base chamber every hour and the experiment was terminated when PO_2 reached approximately 125 mmHg, or after four hours, whichever occurred first.

The electronic flowmeter and both aerial and aquatic oxygen analysers were connected to a MacLab/4e and the signals sampled twice per second. The signals were recorded on Chart using a Power Macintosh (6200/75). The resultant traces were later analysed to determine changes in aquatic PO_2, fluxes in aerial oxygen concentration (%O_2), average flow rates and exact experimental time periods. As a control, changes in PO_2 were also recorded in the respirometer without the presence of an animal and were found to be insignificant.

Partitioning of aquatic oxygen consumption

To determine the relative contribution of the cloaca to aquatic respiration, the respirometry experiment already outlined was repeated for all five animals, but with their cloacas blocked. Coltex Dental lab putty was used to construct a mould for the rear of each animal that included a cavity to accommodate the tail. Once set, the mould was attached to the turtle with tape in such a way that the tail was enclosed and cloacal ventilation was prevented. A small amount of vaseline was smeared around the edge of the mould to minimise water flow between the cloaca and the external environment (validated with the use of food dye to determine that no water was ventilating the cloaca).

Calculating oxygen consumption

Aquatic oxygen consumption (ml O_2 h^{-1}) was calculated using the following formula, modified from King and Heatwole (1994a):

VO_2 (aquatic) = $(\Delta DO \times V) / T \times k$

where,

ΔDO = change in oxygen concentration (ml O_2 l^{-1})

V = volume of water in respirometer (l)

T = experimental time period (h)

k = correction factor for non-standard temperatures

Aerial oxygen consumption (ml O_2 h^{-1}) was calculated using the following formula, taken from Withers (1977):

VO_2 (aerial) = $FR \times (FIO_2 - FEO_2) / 1 - FIO_2$

where,

FR = flow rate of gas through chamber (ml h^{-1})

FIO_2 = fractional concentration of O_2 in the inspiratory gas

FEO_2 = fractional concentration of O_2 in the expiratory gas

The metabolic rate (ml O_2 h^{-1}) of each animal was calculated as follows:

MR = VO_2 (aerial) + VO_2 (aquatic)

Metabolic rate values were scaled to a 1 kg animal using the following scaling equation, from Kinney *et al.* (1977):

$VO_2(s) = VO_2(e) \times (1000^{0.76}) / Mb$

where,

$VO_2(e)$ = experimentally determined metabolic rate (ml O_2 h^{-1})

Mb = mass of animal (g)

The ratio of aquatic O_2 uptake to total metabolic rate (MR) was used to indicate the degree of reliance an animal had on the water as a respiratory medium. That is:

Reliance (aquatic respiration) = 100 x VO_2 (aquatic) / MR

From the partitioning experiments the importance of cloacal O_2 uptake in aquatic respiration was calculated as follows:

Aquatic Reliance (cloaca) = 100 x (VO_2 (Cl op) - VO_2 (Cl bl)) / VO_2 (Cl op)

where,

VO_2 (Cl op) = aquatic oxygen consumption with cloaca open (ml O_2 h^{-1})

VO_2 (Cl bl) = aquatic oxygen consumption with cloaca blocked (ml O_2 h^{-1})

A two-tailed paired t-test was used to determine whether blocking the cloaca had a significant effect on metabolic rate. Similarly, aquatic O_2 uptake was analysed with a two-tailed paired t-test, to determine whether blocking the cloaca had a significant effect on the degree of aquatic respiration.

Results

Aerial and aquatic respiration

The largest turtle (4.3kg) used in the respirometry experiments was the only individual which appeared stressed by the experimental setup. The large body size of this animal inhibited it from moving freely within the respirometer which caused the turtle to panic. As the metabolic rate of this animal would almost certainly have been elevated as a result of the stress, results obtained from the turtle were excluded from statistical analyses.

The average (± standard error) metabolic rate for the four turtles included in statistical analyses was 13.40 ± 1.29 ml O_2 kg^{-1} h^{-1}. The partitioning experiments revealed that the examined individuals demonstrated a high reliance upon aquatic respiration. Average aerial oxygen consumption was 4.23 ± 1.41 ml O_2 kg^{-1} h^{-1}, while aquatic VO_2 averaged 9.19 ± 0.60 ml O_2 kg^{-1} h^{-1}. The ratio of aquatic to total gas exchange revealed that at 22°C, the examined individuals obtained on average 70 ± 8 % of their total oxygen requirements from the water.

The proportional reliance upon aquatic respiration was negatively correlated with body mass over the size range of the four examined animals (0.675 - 3.36kg) and scaled with a mass-exponent of –0.3 (r^2= 0.94; $p < 0.001$). The reliance upon aquatic O_2 uptake increased from approximately 56% in the larger turtles (>2kg), to 88% in the smallest turtle examined (0.675kg).

Partitioning of aquatic oxygen consumption

Blocking the cloaca of the experimental turtles had no significant effect upon metabolic rate ($t = 1.46$, d.f. = 3, $p = 0.108$). Reliance upon aquatic respiration decreased significantly when the cloacas of the experimental turtles were blocked ($t = 3.15$, d.f. = 3, $p < 0.05$). Cloacal O_2 uptake was found to account for 48 ± 12% of total aquatic respiration.

Discussion

The average metabolic rate recorded for freely-diving *E. albagula* during the present study (13.40 ± 1.29 ml O_2 kg^{-1} h^{-1}) is relatively low when compared to O_2 consumption estimates from studies of non-Australian turtle species. Bagatto and Henry (2000) examined biomodal respiration in two species of Central American turtles, the Giant Mexican Musk Turtle *Staurotypus triporcatus* and the White-lipped Mud Turtle *Kinosternon leucostomum*. By measuring aerial and aquatic respiration they calculated that the resting metabolic rate of these two species was 29.2 and 28 ml O_2 kg^{-1} h^{-1}, respectively. Stone *et al.* (1992a) determined O_2 consumption in three freshwater turtles at 24°C and found the soft-shelled turtle *Apalone spiniferus* had the lowest calculated metabolic rate (29.5 ml O_2 kg^{-1} h^{-1}). The mud turtle *Kinosternum subrubrum* and stinkpot *Sternotherus odoratus* were reported as having total O_2 consumption rates of 30 and 35 ml O_2 kg^{-1} h^{-1}, respectively (Stone *et al.* 1992a). Gatten (1980) found a consumption rate of 38 ml O_2 kg^{-1} h^{-1} in the snapping turtle *Chelydra serpentina* at 20°C. The estimates of oxygen consumption from the above-mentioned non-Australian turtles are all 2-3 fold greater than that reported here for *E. albagula*, suggesting adults of this Australian chelid have a low metabolic rate.

The vast majority of research on metabolic rate in Australian freshwater turtles has focused on hatchling (~1-2 months old) and juvenile (~ 1 year old) animals of various species (e.g. Clark *et al.* 2008a, b; Clark *et al.* 2009) (but see King and Heatwole 1994a,b). Due to the small size (all < 150g) of the turtles used in these studies and the significant positive correlation between metabolic rate and body mass in turtles (see Mathie and Franklin 2006), a comparison of the findings of these studies with those of the present would be invalid (mass of turtles in the current study ranged from 0.675 – 3.36 kg). Mathie and Franklin (2006) did examine aerial and aquatic respiration in *E. albagula* but did not state quantified metabolic rates for any of the sizes classes examined (hatchlings, juveniles, adult males, adult females).

Perhaps of more interest than the absolute value of metabolic rate is the ratio of aquatic O_2 uptake to total oxygen consumption. This ratio is a good indication of the degree of reliance an animal has on the water as a respiratory medium. In this study *E. albagula* obtained on average 70 ± 8 % of its total oxygen requirements from normoxic water at 22°C, with the reliance upon aquatic O_2 uptake increasing from approximately 56% in the larger turtles (>2kg), to 88% in the smallest turtle examined (0.675kg). Most estimates of reliance upon aquatic oxygen uptake in non-Australian turtles are considerably lower than that reported here, with values ranging from 5% (snapping turtles; Gatten 1980) to 38% (soft-shelled turtles; Stone *et al.* 1992a).

Numerous studies have assessed reliance upon aquatic respiration in Australian turtles. King and Heatwole (1994a) report that in the congeneric species *E. latisternum*, aquatic respiration accounts for 27% of total oxygen consumption at 20°C. Of most relevance to the current study is the work of Mathie and Franklin (2006), who also examined the diving physiology of *E. albagula*. Among adult turtles they found a lower average reliance upon aquatic gas exchange (17.0 ± 3.0%) and a maximum reliance of approximately 40%. The large difference in the estimate of mean reliance upon aquatic respiration may be partly due to the small sample size in the current study (n = 4) and the inclusion of a sub-adult turtle (0.675kg), which obtained an impressive 88% of its oxygen demands in this way. However, even without the inclusion of this animal, the average reliance upon aquatic respiration in the remaining three adult turtles exceeded 60%. This incredible capacity to respire aquatically likely facilitates the prolonged dives (> 3 hrs) that *E. albagula* has been found to occasionally undertake (FitzGibbon 1998; Gordos *et al.* 2007; Clark *et al.* 2008a; Storey *et al.* 2008). Mathie and Franklin (2006) examined a wide size range of *E. albagula* and reported a significant negative correlation between body mass and capacity for aquatic respiration (mass-exponent = -0.23), although there was large variation in percent aquatic oxygen consumption among hatchlings and juveniles (6 – 100%). Similarly, despite the small sample size in the current study, a significant negative correlation was found between body mass and reliance upon aquatic respiration with a similar mass-exponent (-0.3). These studies highlight the heightened ability of small turtles to utilise aquatic respiration which is likely attributable to their higher mass-specific cloacal bursae surface area (see Mathie and Franklin 2006).

Among Australian chelids, *R. leukops* is considered to have the most specialised cloacal bursae and consequently, the most developed ability to respire aquatically and undertake prolonged dives (see Gordos and Franklin 2002; Priest and Franklin 2002; Clark *et al.* 2008a). Priest (1997) has shown that adult *R. leukops* have an average reliance on aquatic O_2 exchange of approximately 40%, with some individuals obtaining up to 69% of their oxygen demands in this way. However, Priest (1997) notes that the examined *R. leukops* appeared very stressed by the respirometry setup and appeared to spend considerably more time at the water surface (respiring aerially) than was considered normal. For this reason, the stated capability of adult *R. leukops* to respire aquatically is likely an underestimate and the true value may actually be closer to, if not exceeding, the estimates derived here for *E. albagula*.

The primary aim of the current study was to test the hypothesis that the cloacal bursae of *E. albagula* are the main site of aquatic respiration, being more important in underwater gas exchange than either the buccopharynx or skin. Only one other study of an Australian chelid has partitioned the contribution of extrapulmonary respiratory sites to overall aquatic O_2 uptake, which found that the buccopharynx was primarily responsible (King and Heatwole 1994a). Despite this, many other studies of the diving physiology of Australian chelids seem to presume that the cloacal bursae are the main site of aquatic gas exchange. This hypothesis was assessed in the current study by determining the reliance upon aquatic respiration in freely-diving turtles with and without their cloacas blocked. We found that *E. albagula* obtains 48% of its aquatic oxygen uptake via the cloaca. Aquatic oxygen consumption was not further partitioned to determine the importance of buccopharyngeal or cutaneous uptake due to technical difficulties in isolating these areas without causing a significant elevation of metabolic rate due to imposed stress. In the partitioning experiments custom-made putty moulds were used to block cloacal gas exchange and overall metabolic rate was not significantly altered during these experiments.

Although the relative contribution of the buccopharynx and skin to aquatic respiration were not quantified, two reasons are provided to support the assertion that the cloaca is the main site of aquatic respiration in *E. albagula*. Firstly, the buccopharynx or skin could only be more important than the cloaca if one or the other of these sites accounted for less than approximately

3.4% of total aquatic O_2 uptake, leaving the remaining 49% attributable to the third avenue. This seems unlikely especially given that in the congeneric turtle *E. latisternum*, the least important site of aquatic respiration (the skin) still accounted for 18% aquatic O_2 uptake (King and Heatwole 1994a: buccopharynx 49%, cloaca 33%). Secondly, as King and Heatwole (1994a) identify, the importance of the buccopharynx and the skin may have been overestimated somewhat in relation to that of the cloaca, as the turtles may have compensated for the blocking of one avenue of aquatic respiration by increasing oxygen uptake through the others. As a result, the calculated contribution of the cloaca to total aquatic respiration may have been underestimated in the current study, suggesting it may actually account for more than 50% of aquatic O_2 uptake. King and Heatwole (1994a) propose it is more likely that increased pulmonary uptake would be used to make any respiratory adjustments when the cloaca is blocked. However, because aerial O_2 consumption was not monitored in their study they were unable to verify this prediction. In the present study aerial oxygen consumption was monitored throughout the partitioning experiments and was indeed found to increase in *E. albagula* when their cloacas were blocked. While this does not disprove the possibility that the reliance upon the skin and buccopharynx was increased when the cloaca was blocked, it does suggest that the contribution of the cloaca to aquatic respiration has not been grossly underestimated. However, the results of the partitioning experiments in the present study and King and Heatwole (1994a), suggest it should not be assumed that the buccopharynx and skin play only a minor role in aquatic respiration among Australian chelids, and that further investigation of this is warranted.

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References

Andersen, H.T. 1966. Physiological adaptations in diving vertebrates. *Physiological Reviews* **46**: 212-243.

Bagatto, B., Guyer, C., Hauge, B. and Henry, R.P. 1997. Bimodal respiration in two species of Central American turtles. *Copeia* **1997**: 834-839.

Bagatto, B. and Henry, R.P. 2000. Bimodal respiration and ventilatory behavior in two species of Central American turtles: effects of forced submergence. *Comparative Biochemistry and Physiology Part A* **126**: 57-63.

Belkin, D.A. 1968. Aquatic respiration and underwater survival of two freshwater turtle species. *Respiration Physiology* **4**: 1-14.

Caligiuri, M., Robina, E.D., Hance, A.J., Robina, D.A. Lewistona, N. and Theodore, J. 1981. Prolonged diving and recovery in the freshwater turtle, *Pseudemys* scripta – 2. Magnitude of depression of O_2 requirements and the relation to body O_2 stores. *Comparative Biochemistry and Physiology Part A: Physiology* **70**: 365-369.

Cann, J. and Legler, J.M. 1994. The Mary River tortoise: a new genus and species of short-necked Chelid from Queensland, Australia (Testudines: Pleurodira). *Chelonian Conservation and Biology* **1**: 81-96.

Clark, N.J., Gordos, M.A. and Franklin, C.E. 2008a. Diving behaviour, aquatic respiration and blood respiratory properties: a comparison of hatchling and juvenile Australian turtles. *Journal of Zoology* **275**: 399-406.

Clark, N.J., Gordos, M.A. and Franklin, C.E. 2008b. Thermal plasticity of diving behaviour, aquatic respiration, and locomotor performance in the Mary River Turtle *Elusor macrurus*. *Physiological and Biochemical Zoology* **81**: 301-309.

Clark, N.J., Gordos, M.A. and Franklin, C.E. 2009. Implications of river damming: the influence of aquatic hypoxia on the diving physiology and behaviour of the endangered Mary River turtle. *Animal Conservation* **12**: 147-154.

Dunson, W.A. 1960. Aquatic respiration in *Trionyx spinifer asper*. *Herpetologica* **16**: 277-283.

FitzGibbon, S.I. 1998. *The diving physiology and dive behaviour of an undescribed turtle (Elseya sp.) from the Mary River, Queensland*. BSc Honours thesis, The University of Queensland, Brisbane.

Gatten, R.E. 1980. Aerial and aquatic oxygen uptake by freely-diving snapping turtles (*Chelydra serpentina*). *Oecologia* **46**: 266-271.

Gatten, R.E. 1981. Anaerobic metabolism in freely diving painted turtles (*Chrysemys picta*). *Journal of Experimantal Zoology* **216**: 377-385.

Gatten, R.E. 1984. Aerobic and anaerobic metabolism of freely-diving loggerhead musk turtles (*Sternotherus minor*). *Herpetologica* **40**: 1-7.

Girgis, S. 1961. Aquatic respiration in the common Nile turtle, *Trionyx triunguis* (Forskal). *Comparative Biochemistry and Physiology* **3**: 206-217.

Gordos, M.A. 2004. *Diving physiological ecology of the bimodally respiring freshwater turtle, Rheodytes leukops*. PhD thesis, The University of Queensland, Brisbane.

Gordos, M.A. and Franklin, C.E. 2002. Diving behaviour of two Australian bimodally respiring turtles, *Rheodytes leukops* and *Emydura macquarii*, in a natural setting. *Journal of Zoology* **258**: 335-342.

Gordos, M.A., Hamann, M., Schauble, C.J. and Franklin, C.E. 2007. Diving behaviour of *Elseya albagula* from a naturally flowing and hydrologically altered habitat. *Journal of Zoology* **272**: 458-469.

Jackson, D.C. 1968. Metabolic depression and oxygen depletion in diving turtle. *Journal of Applied Physiology* **24**: 503

Jackson, D.C., Allen, J. and Strupp, P. 1976. The contribution of non-pulmonary surfaces to CO_2 loss in 6 species of turtle at 20°C. *Comparative Biochemistry and Physiology* **55A**: 243-246.

Jackson, D.C., Rauer, E.M., Feldman, R.A. and Reese, S.A. 2004. Avenues of extrapulmonary oxygen uptake in western painted turtles (*Chrysemys picta belli*) at 10 degrees C. *Comparative Biochemistry and Physiology* **139**: 221-227.

King, P. and Heatwole, H. 1994a. Partitioning of aquatic oxygen uptake among different respiratory surfaces in a freely diving pleurodiran turtle, *Elseya latisternum*. *Copeia* **3**: 802-806.

King, P. and Heatwole, H. 1994b. Non-pulmonary respiratory surfaces of the Chelid turtle *Elseya latisternum*. *Herpetologica* **50**: 262-265.

Kinney, J.L., Matsuura, D.T. and White, F.N. 1977. Cardiorespiratory effects of temperature in turtle, *Pseudemys floridana*. *Respiratory Physiology* **31**: 309-325.

Legler, J.M. 1987. Morphology and physiology of the Chelonia. Pp. 108-119 in *Fauna of Australia Vol 2A: Amphibia & Reptilia*, edited by C.J. Glasby, G.J.B. Ross and P.L. Beesley. Australian Government Publishing Service, Canberra, ACT.

Legler, J.M. and Cann, J. 1980. A new genus and species of chelid turtle from Queensland, Australia. *Contributions to the scientific Natural History Museum Los Angeles County* **324**: 1-18.

Legler, J.M. and Georges, A. 1987. Family Chelidae. Pp. 142-152 in *Fauna of Australia Vol 2A: Amphibia & Reptilia*, edited by C.J. Glasby, G.J.B. Ross and P.L. Beesley. Australian Government Publishing Service, Canberra, ACT.

Limpus, C.J., Limpus, D.J. and Hamann, M. (2002). Freshwater turtle populations in the area to be flooded by the Walla Weir, Burnett River, Queensland: baseline study. *Memoirs of the Queensland Museum* **48**: 155-168.

Maina, J.N. 2002. Structure, function and evolution of the gas exchangers: comparative perspectives. *Journal of Anatomy* **201**: 281-304.

Mathie, N.J. and Franklin, C.E. 2006. The influence of body size on the diving behaviour and physiology of the bimodally respiring turtle, *Elseya albagula*. *Journal of Comparative Physiology B* **176**: 739-747.

Priest, T.E. 1997. *Bimodal respiration and dive behaviour of the Fitzroy River Turtle, Rheodytes leukops*. Honours thesis, The University of Queensland, Brisbane.

Priest, T.E. and Franklin, C.E. 2002. Effect of water temperature and oxygen levels on the diving behaviour of two freshwater turtles: *Rheodytes leukops* and *Emydura macquarii*. *Journal of Herpetology* **36**: 555-561.

Root, R.W. 1949. Aquatic respiration in the musk turtle. *Physiological Zoology* **22**: 172-178.

Santos, E.A., Laitano, S.Y.T. and Genofre, G.C. 1990. Diving physiology of *Chrysemys dorbignyi*. *Comparative Biochemistry and Physiology* **95A**: 229-236.

Schmidt-Nielsen, K. (1983). *Animal Physiology: Adaptation and Environment*. Cambridge University Press, New York, USA.

Stone, P.A., Dobie, J.L. and Henry, R.P. 1992a. Cutaneous surface area and bimodal respiration in Soft-shelled (*Trionyx spiniferus*), Stinkpot (*Sternotherus odoratus*), and Mud Turtles (*Kinosternon subrubrum*). *Physiological Zoology* **65**: 311-330.

Stone, P.A., Dobie, J.L. and Henry, R.P. 1992b. The effect of aquatic O_2 levels on diving and ventilatory behavior in soft-shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*), and mud turtles (*Kinosternon subrubrum*). *Physiological Zoology*, **65**: 331-345.

Storey, E.M., Kayes, S.M., De Vries, I. and Franklin, C.E. 2008. Effect of water depth, velocity and temperature on the surfacing frequency of the bimodally respiring turtle *Elseya albagula*. *Functional Ecology* **22**: 840-846.

Smith, E.N. and De Carvalho, M.C. Jnr. 1985. Heart rate response to threat and diving in the ornate box turtle, *Terepene ornata*. *Physiological Zoology* **58**: 236-241.

Thomson, S. Georges, A. and Limpus, C.J. 2006. A new species of freshwater turtle in the genus Elseya (Testudines: Pleurodira) from central coastal Queensland, Australia. *Chelonian Conservation and Biology* **5**: 74-86.

Tucker, A.D., Limpus, C.J., Priest, T.E., Cay, J., Glen, C. and Guarino, E. (2001). Home ranges of Fitzroy River turtles (*Rheodytes leukops*) overlap riffle zones: potential concerns related to river regulation. Biological Conservation **102**: 171-181.

Wang, T. and Hicks, J.W. 1996. Cardiorespiratory synchrony in turtles. *Journal of Experimental Biology* **199**: 1791-1800.

Ware, S.K. 1993. Cardiac responses of the turtle (*Trachemys scripta elegans*) to voluntary diving and to forced submersion. *Comparative Biochemistry and Physiology* **105A**: 751-755.

Withers, P.C. 1977. Measurement of VO_2, VCO_2, and evaporative water-loss with a flow-through mask. *Journal of Applied Physiology* **42**: 120-123.